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Two new species of *Heth* Cobb, 1898 (Nematoda, Rhigonematidae), from South American Diplopods

par Martin L. Adamson

Abstract. — Two new species of *Heth* Cobb, 1898 (Rhigonematidae) are described from South American diplopods : *H. bifidispiculum* n. sp. from Venezuela and *H. mauriesi* n. sp. from Martinique. In cephalic and cervical cuticular ornamentation in the female the new species resemble *H. duvidosum* Artigas, 1929, and *H. perarmatum* Dollfus, 1952, from Sao Paulo, Brazil, described only on the basis of female morphology. The new species differ from *H. perarmatum* in that, except for the two lateral spine pairs, all spines in the cervical collar are of similar size. Types of *H. duvidosum* were not available and the species has not been described in enough detail to permit comparison. *Heth mauriesi* n. sp. differs from *H. bifidispiculum* n. sp. in vulvar structure and number of somatic papillae in the female and in spicular structure and disposition of caudal papillae in the male. The cephalic end of the female including buccal capsule and associated musculature is described and compared with that observed in the male. As has been observed in other nematodes, the morphology of the male is more primitive than that of the female.

Résumé. — Description de deux espèces nouvelles du genre *Heth* Cobb, 1898, chez les Diplopodes sud-américains : *H. bifidispiculum* n. sp. du Vénézuéla et *Heth mauriesi* n. sp. de la Martinique. Par l'ornementation cuticulaire de l'extrémité antérieure de la femelle, les deux espèces sont proches de *H. duvidosum* Artigas, 1929, et *H. perarmatum* Dollfus, 1952, de São Paulo, Brésil, dont la femelle seule est connue. Elles diffèrent de *H. perarmatum* par le fait que, à l'exception des deux paires d'épines latérales, les épines du collier cervical sont de même taille, alors qu'elles sont de tailles différentes chez *H. perarmatum*. Les types de *H. duvidosum* semblent ne plus exister et la description de cette espèce n'est pas assez détaillée pour permettre une comparaison. *H. mauriesi* n. sp. se distingue de *H. bifidispiculum* n. sp. par la structure de la vulve et le nombre des papilles somatiques chez la femelle, et par la forme des spicules et la position des papilles génitales chez le mâle. L'extrémité céphalique de la femelle (capsule buccale et muscles) est décrite et comparée à celle du mâle. Comme c'est le cas chez d'autres espèces de Nématodes, la morphologie du mâle est plus primitive que celle de la femelle.

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An examination of intestines of some diplopods in the collection of the Muséum national d'Histoire naturelle (Paris) revealed the presence of two new species of *Heth* Cobb, 1898 (Nematoda, Rhigonematidae), namely, *Heth bifidispiculum* n. sp. and *Heth mauriesi* n. sp. *Heth* is characterized by the cephalic end in the female which is highly modified and ornamented with cuticular spines. The form and disposition of these spines have been used to distinguish species, but species have generally been inadequately described and the morphology of the cephalic end is not understood yet. In the present study, special attention has been given to the cephalic extremity in both sexes in an effort to determine homologies and possible functions.

MATERIALS AND METHODS. — Diplopods had been fixed and stored in 70 % ethanol prior to dissection. The posterior portion of the intestine was opened and nematodes were collected and stored in 70 % ethanol before being cleared and studied in lactophenol.

1. **Heth bifidispiculum** n. sp.

MATERIAL EXAMINED. — Nematodes came from a single specimen of *Rhinocricus flavocinctus* Karsch [1] from the diplopod collection in the national Museum of natural History in Paris (Zoologie— Arthropodes : boeal H42, tube DXIII). The diplopod was collected in Colony Tovar, Venezuela. Nematode types have been deposited in the parasite collection of the Paris Museum (Zoologie — Vers : 22 RA).

DESCRIPTION

Somatic papillae present throughout length of body. Body cuticle faintly striated. Excretory system consisting of inconspicuous pore leading to long tubular terminal duct (fig. 1, E, F). Terminal duct running posteriorly and expanding to form large cell body (sinus cell) embedded in right sublateral hypodermal cord. Intestine looped in body cavity.

MALE (fig. 1)

Lips absent. Mouth opening surrounded by outer ring of four submedian papillae and two amphids, and inner ring of six small papillae (fig 1, J). Tissue surrounding amphids raised slightly (fig. 1, G).

Anterior portion buccal cavity with round to oval lumen lined by thin layer of smooth cuticle continuous with body cuticle (fig. 1, K). Posterior portion of buccal cavity with triangular lumen lined by thick buccal capsule with one dorsal and two subventral swellings (fig. 1, H, I, L). Swellings striated in apical and side view and each with a cuticular structure projecting anteriorly into buccal cavity. Cuticular projections featherlike in side view but in apical view seen to consist of central stalk around which cuticular lamellae are arranged like petals of a flower. One pair subdorsal and one pair subventral body wall muscles attached to dorsal and ventral sides of buccal capsule.

Coelomocytes with foamy cytoplasm : one pair near flexure of testis, one unpaired near base of œsophageal corpus and one unpaired near junction of seminal vesicle and vas deferens (fig. 1, A).

Spicule with two heads and single shaft (fig. 1, B, C, D). Shaft with median ventral blade. Distal end of spicule curving sharply ventrally and ending in T-shaped extremity.

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[1] HOFFMAN (1960) restricted considerably the definition of *Rhinocricus*. If his scheme is followed this species would become *Anadenobolus flavocinctus*.

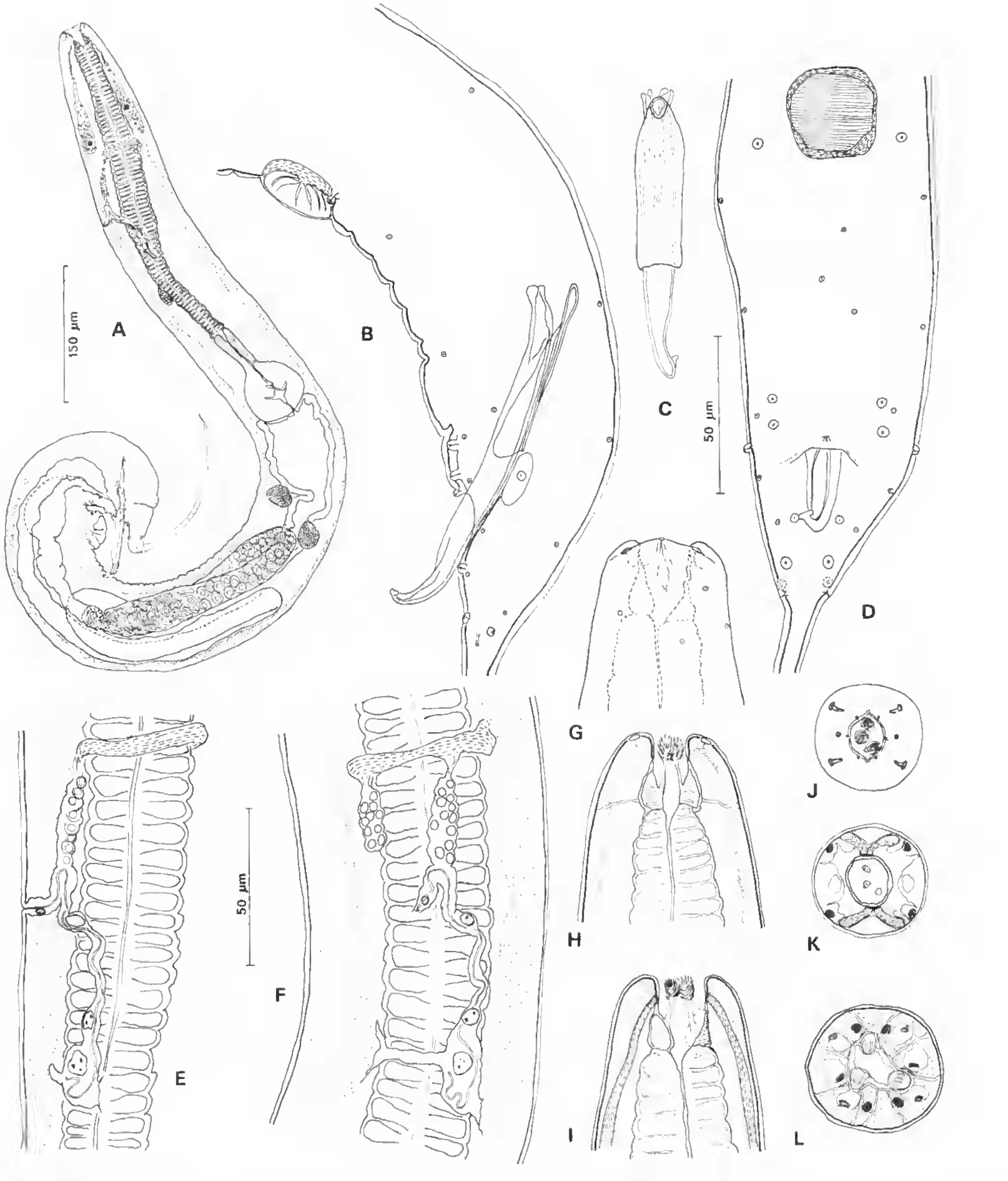

Fig. 1. — *Heth bifidispiculum* n. sp., male. A, entire worm, lateral view ; B, caudal extremity, lateral view ; C, spicule and gubernaculum, dorsal view ; D, caudal extremity, ventral view ; E-F, excretory system, lateral and ventral views ; G, cephalic extremity, superficial lateral view ; H, cephalic extremity, ventral view ; I, cephalic extremity, lateral view ; J, cephalic extremity, apical view ; K, section through buccal cavity at level of attachment of subdorsal and subventral muscles ; L, section through base of buccal cavity. (A = 150 µm scale ; B to L = 50 µm scale.)

Plate of thickened smooth cuticle present in dorsal wall of spicular sheath just before junction with cloaca.

Prominent ventral sucker present encircled by ring of muscle. Fifteen genital papillae : — one pair subventral near level of posterior edge of ventral sucker ; — two pairs subventral just anterior to level of anus ; — median unpaired papilla on anterior anal lip ; — one pair lateral adanal ; — two pairs subventral and one pair dorsolateral postanal.

Many somatic papillae much smaller than genital papillae, arranged in two subdorsal and two subventral rows, occasionally ventrally and laterally. Phasmids just behind last pair genital papillae.

FEMALE (fig. 2, 3)

Two prominent pseudolabia present, anterior end of each a broad cuticular plate, roughly trapezoidal in apical view, overhanging base of pseudolabium on dorsal, ventral and inside edges (fig. 2, A ; 3, C, E). Pseudolabial plates touching but not connected at their dorsal and ventral corners. Body cuticle at base of pseudolabia on dorsal and ventral sides forming flange which mirrors that formed by pseudolabial plates.

Two cuticular struts present, one subdorsal and one subventral, running up sides of each pseudolabium and fanning out along dorsal and ventral edges of pseudolabial plates (labelled " a " in fig. 2, A, B ; 3, A). Four similar struts, two subdorsal and two subventral supporting lower flange of body cuticle (labelled " b " in fig. 2, B ; 3, A). Proximal ends of the two struts in each quadrant meeting each other at right angles and third smaller cuticular component ("c", fig. 2, B ; 3, A), triangular and striated in side view supporting the junction of the two struts.

Pseudolabia apposed such that mouth opening divided into three parts : (1) apical dorsoventral slit ; (2) dorsal transverse slit ; (3) ventral transverse slit. Edges of each part of mouth opening reinforced and lined by cuticular comb-like formation ; teeth of these combs projecting into mouth opening.

Amphidial openings cuticularly reinforced, on pseudolabial plates. Four cephalic papillae present, at base of pseudolabia just inside mouth opening, one at each of its extreme lateral corners (fig. 2, B).

Buccal cavity and capsule (fig. 2, F-J) divided into three parts :

(1) anterior segment between pseudolabia ;

(2) thick cuticular ring circular in cross-section surrounding subtriangular buccal cavity ; this ring, in turn, divided into anterior segment extending forward on lateral sides to line pseudolabia, and posterior segment with one dorsal and two subventral lappet — like formations ; each lappet with many fine cuticular hairs on posterior surface and arising from cuticular swelling in buccal capsule.

(3) long segment with oval lumen lined by thin layer of striated cuticle surrounded by hypodermis.

Six pairs of muscles present attached to ring of cuticle lining second part of buccal cavity (fig. 3, A, B) :

— on each side, pair of lateral muscles running to body cuticle in cervical region ;

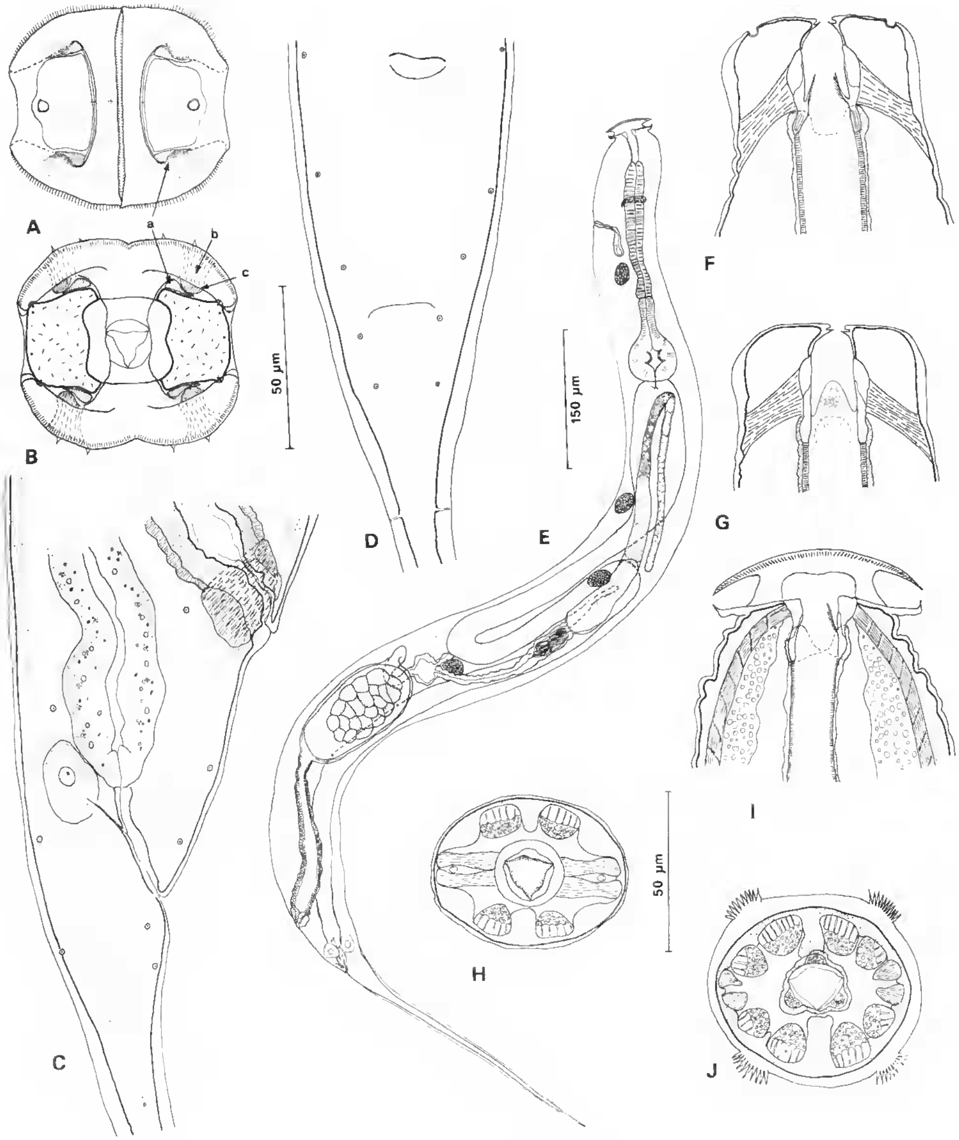

Fig. 2. — *Heth bifidispiculum* n. sp., female. A-B, cephalic extremity, apical view. A, superficial ; B, section through base of pseudolabia. a, b and c, cuticular struts supporting pseudolabia and edges of mouth ; C-D, caudal extremity, lateral and ventral views ; E, entire worm, lateral view ; F-G, cephalic extremity, ventral view, G, slightly deeper than F, showing dorsal lappet in frontal view ; H, section through buccal cavity at point of attachment of lateral muscle pairs ; I, cephalic extremity, lateral view showing dorsal lappet in profile ; J, section through buccal cavity at level of dorsal and subventral swellings. (C = 150 µm scale ; the rest = 50 µm scale.)

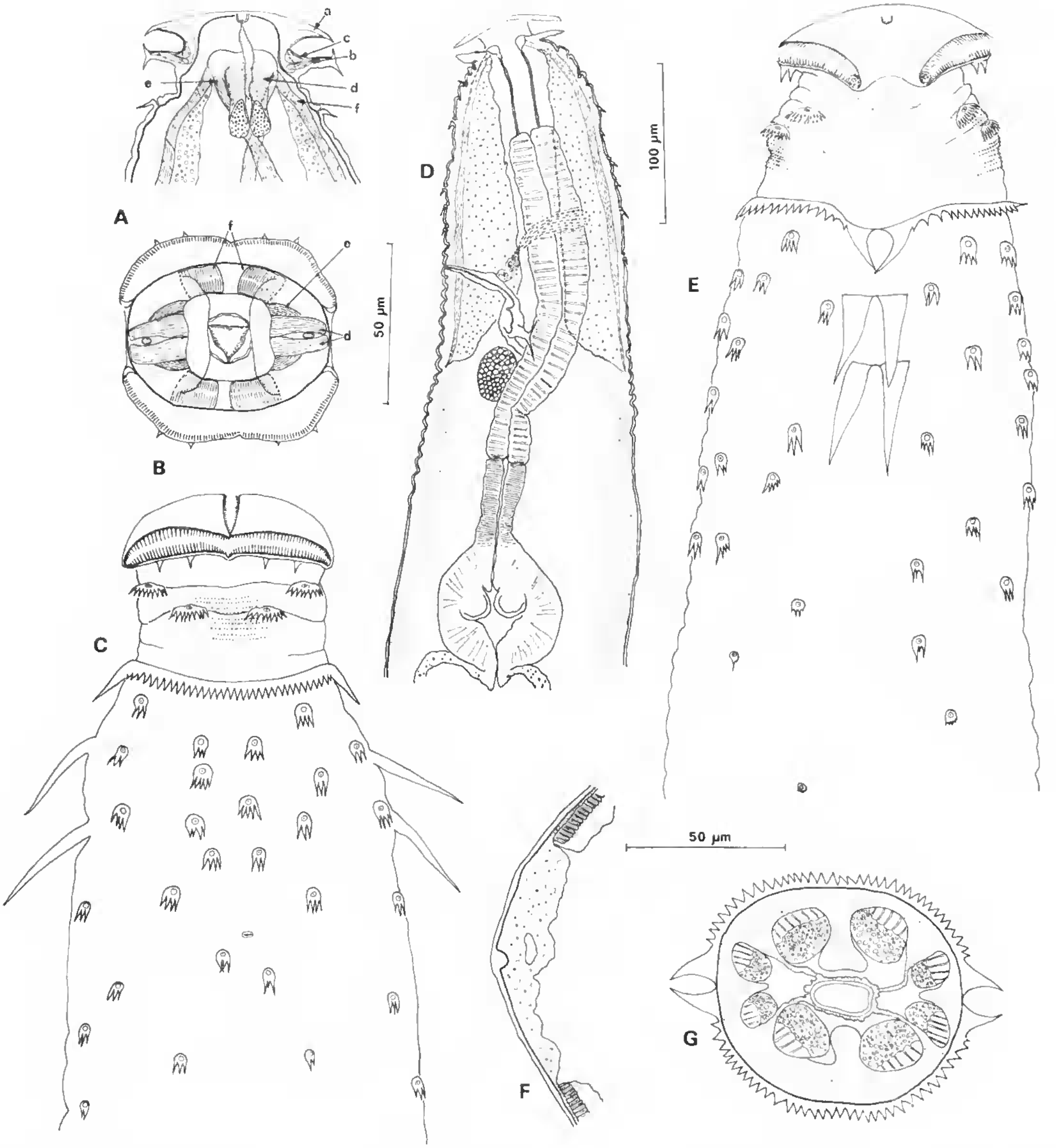

Fig. 3. — *Heth. bifidispiculum* n. sp., female. A-B, cephalic extremity in lateral and apical view showing musculature of buccal cavity. a, b and c, cuticular struts supporting pseudolabia and edges of mouth. d, e and f, muscles attached to buccal cavity : d, lateral pair, e, sublateral pair ; f, subdorsal pair ; C, anterior extremity, ventral view, showing cuticular ornamentation ; D, œsophageal region, lateral view ; E, anterior extremity lateral view showing cuticular ornamentation ; F, section through lateral cord showing cuticular thickening ; G, section through cervical collar and posterior section of buccal cavity. (D = 100 µm scale ; the rest = 50 µm scale.)

— also on each side, dorsolateral and ventrolateral body wall muscles running anteriorly and crossing just posterior to lateral muscles before attaching to buccal capsule ;

— subdorsal and subventral pairs of body wall muscles attaching to dorsal and ventral sides of buccal capsule.

Anterior extremity ornamented with many cuticular formations disposed as follows (fig. 3, C, E) :

— four posteriorly-directed spines on posterior edges of dorsal and ventral transverse sections of mouth opening ;

— four groups of cuticular spines arranged in two pairs, one posterior to the other in the cervical region. Each spine group with central nerve ending and nine to eleven posteriorly-directed spines sharing common base ;

— fifteen to twenty transverse rows of tiny spines on dorsal and ventral sides in cervical region ;

— prominent cervical collar with seventy to eighty posteriorly-directed spines sharing common base, interrupted laterally by two much larger spines (fig. 3, G) ;

— on each side two pairs of large spines located in tandem posterior to large lateral spines in cervical collar ;

— many small button-like formations each with a central nerve ending and two to eight spines on their posterior borders, arranged in six irregular longitudinal rows on subdorsal and subventral sides of body. These beginning posterior to cervical collar, becoming less numerous and smaller posteriorly, losing their spines near level of isthmus and continuing to anal region as somatic papillae.

Reproductive system consisting of paired ovaries and oviducts and common seminal receptacle, uterus and vagina. Eggs (71-91 µm wide and 180-215 µm long), not numerous, thin-shelled and containing embryo in early stage of development. Four coelomocytes : one just behind sinus cell of excretory system, two associated with ovaries and one near junction of oviducts and seminal receptacle.

Somatic papillae arranged in two subdorsal and two subventral rows, rarely lateral. Lateral cuticular thickening present running from level of isthmus to level of anus (fig. 3, F).

Dimensions

Holotype male : Length 1.54 mm. Maximum width 103 µm near midbody. Width of head 40 µm. Buccal cavity 27 µm, œsophageal corpus 380 µm and isthmus 57 µm long. Bulb 68 µm long and 64 µm wide. Nerve ring 150 µm and excretory pore 220 µm from anterior extremity. Ventral sucker 28 µm in diameter, 178 µm anterior to anus. Spicule 114 µm, gubernaculum 61 µm and tail 246 µm long.

Allotype female : Length 2.06 mm. Maximum width 141 µm near midbody. First part buccal cavity 24 µm, second and third part buccal cavity 47 µm, œsophageal corpus 201 µm and isthmus 54 µm long. Œsophageal bulb 79 µm long and 82 µm wide. Nerve ring 127 µm and excretory pore 162 µm from anterior extremity. Vulva 94 µm anterior to anus. Tail 498 µm long.

Paratypes males (five specimens) : Length 1.26-1.62 mm. Maximum width 94-112 µm. Head 36-43 µm wide. Buccal cavity 25-33 µm, œsophageal corpus 329-394 µm and isthmus

47-57 μm long. Œsophageal bulb 60-73 μm long and 61-69 μm wide. Nerve ring 129-159 μm and excretory pore 193-235 μm from anterior extremity. Ventral sucker 35-41 μm in diameter, 141-233 μm anterior to anus. Spicule 105-135 μm, gubernaculum 51-64 μm and tail 222-266 μm long.

Paratype females (two specimens) : Length 1.88, 2.08 mm. Maximum width 131, 139 μm. First part buccal cavity 19, 20 μm, second and third part buccal cavity 57, 52 μm long. Œsophageal corpus 211, 192 μm and isthmus 54, 54 μm long. Œsophageal bulb 81, 84 μm long and 75, 81 μm wide. Nerve ring 124, 130 μm and excretory pore 158, 158 μm from anterior extremity. Vulva 97, 80 μm anterior to anus and tail 342, 499 μm long.

Discussion

In cephalic and cervical cuticular ornamentation of the female, *Heth bifidispiculum* n. sp. closely resembles *H. duvidosum* Artigas, 1929, and *H. perarmatum* Dollfus, 1952, from diplopods from Sao Paulo, Brazil. These latter species are known only by female morphology and this has been inadequately described. Two slides labelled *H. perarmatum* are in the parasite collection of the Paris Museum (BD 8). The worms are in poor condition but can be distinguished from the present species since spines in the cervical collar of *H. perarmatum* are of variable size (Dollfus, 1952). Except for two lateral spine pairs, spines in the cervical collar of *H. bifidispiculum* are of similar size. In addition, there are more spines in the spine groups between the head and cervical collar in Dollfus' specimens (twelve to fifteen in *H. perarmatum* compared with nine to eleven in *H. bifidispiculum*).

Artigas (1929) described *H. duvidosum* from a joint infection with *H. spinosum* Artigas, 1929, and was unable to pair males and females of the two species ; he described the two species on the basis of female morphology and described the males separately as *Heth* spp. Unfortunately, the only female at his disposal had lost part of its anterior end. Type specimens of *H. duvidosum* no longer exist according to Kloss (1965.) The species is not described in sufficient detail to permit comparison with the present material and the latter is therefore described as new.

2. **Heth mauriesi** n. sp.

(Fig. 4, 5, 6)

Material examined. — Nematodes were collected from *Anadenobolus politus* (Porat, 1889) from Martinique. Types of the nematodes have been deposited in the parasite collection of the Paris Museum (Zoologie — Vers 13 RA).

This species is extremely close to *H. bifidispiculum*. However, males of *H. mauriesi* differ in the following respects :

— the spicule terminates in a simple point (fig. 5, F to G) ;

— the most anterior pair of genital papillae is located twenty to thirty μm posterior to level of posterior edge of the ventral sucker (fig. 5, D-E) ;

— the dorsolateral papilla pair is located at the same level or slightly anterior to the last pair of subventral papillae (in *H. bifidispiculum* the dorsolateral papillae are slightly posterior to the last pair of subventral papillae).

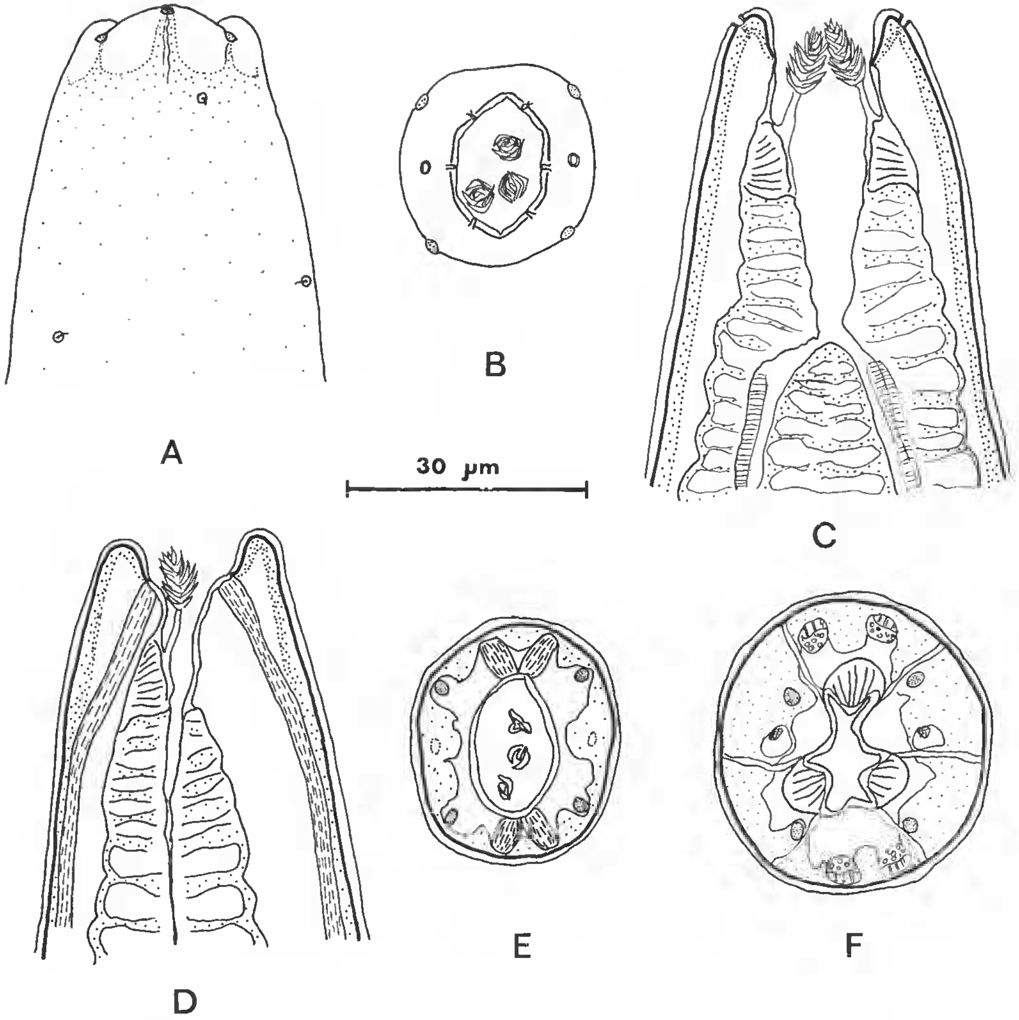

Fig. 4. — *Heth mauriesi* n. sp., male cephalic extremity. A, superficial view, lateral ; B, superficial apical view ; C, ventral view showing subventral cuticular projections ; D, lateral view ; E, section through buccal cavity at point of attachment of subdorsal and subventral muscles ; F, section through base of buccal cavity.

Females of the two species differ as follows :

— the posterior lip of the vulva is extremely prominent in *H. mauriesi* and the body tapers abruptly posterior to the vulva (fig. 5, B-C) ;

— somatic papillae are more numerous on *H. mauriesi* ; this is most obvious posterior to the vulva ;

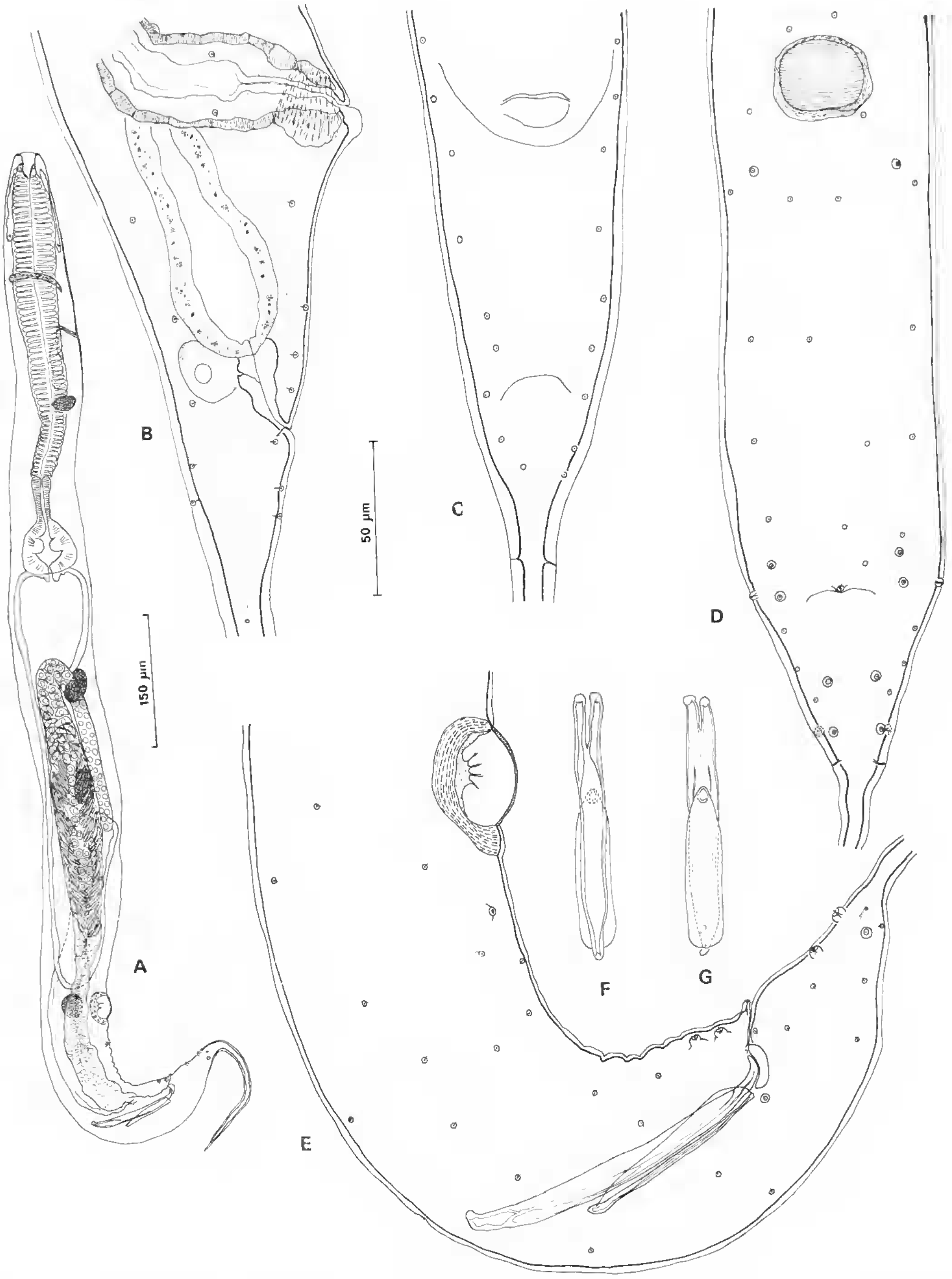

FIG. 5. — *Heth mauriesi* n. sp. A, male, entire, lateral view ; B-C, caudal extremity of female, lateral and ventral views ; D-E, caudal extremity of male, ventral and lateral views ; F-G, spicule and gubernaculum, ventral and dorsal views. (A = 150 µm scale ; B to G = 50 µm scale.)

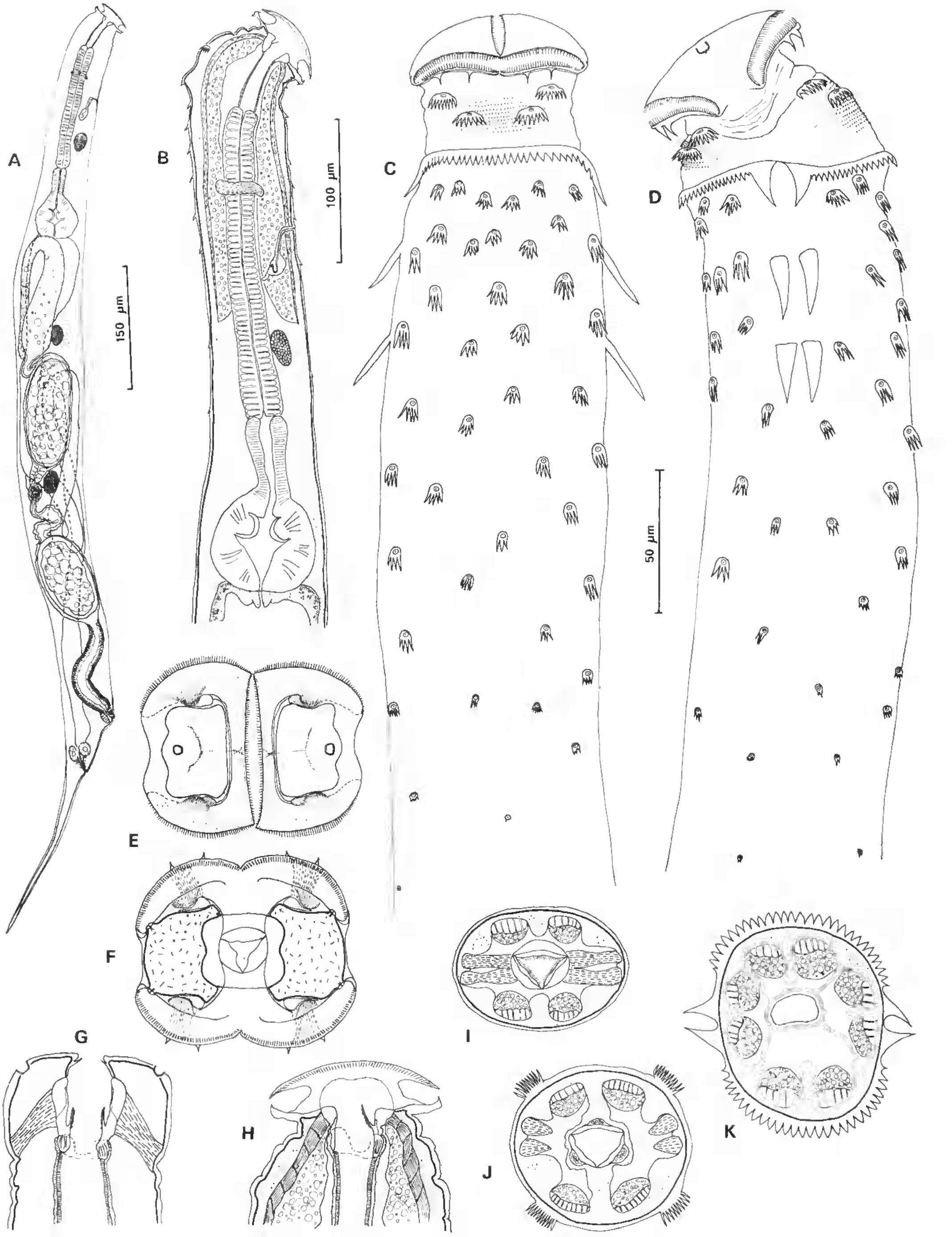

Fig. 6. — *Heth mauriesi* n. sp., female. A, entire worm, lateral view ; B, œsophageal region, lateral view ; C-D, anterior extremity, dorsal and lateral view ; E, apical view, superficial ; F, section through base of pseudolabia ; G, cephalic extremity, ventral view showing subventral lappets in profile ; H, cephalic extremity, lateral view showing dorsal lappet in profile ; I, section through buccal cavity at point of attachment of subdorsal and subventral muscles ; J, section through buccal cavity at level of dorsal and subventral swellings ; K, section at level of cervical collar. (A = 150 µm scale ; B = 100 µm scale ; C to K = 50 µm scale.)

— there are fewer spines in the cervical collar of *H. mauriesi* (i.e. 58-65 as compared with 70-80 in *H. bifidispiculum*) (fig. 6, K) ;

— the œsophageal corpus is cylindrical in *H. mauriesi* (fig. 6, B), whereas it narrows and then broadens again before joining with the isthmus in *H. bifidispiculum*.

Dimensions

Holotype male : Length 1.68 mm. Maximum width 97 µm hear midbody. Head 30 µm wide. Buccal cavity 26 µm, œsophageal corpus 449 µm and isthmus 60 µm long. Œsophageal bulb 68 µm long and 69 µm wide. Nerve ring 161 µm and excretory pore 251 µm from anterior extremity. Ventral sucker 33 µm in diameter, 241 µm anterior to anus. Spicule 115 µm, gubernaculum 62 µm and tail 201 µm long.

Allotype female : Length 1.65 mm. Maximum width 107 µm near midbody. First part buccal cavity 16 µm, second and third part buccal cavity 59 µm, œsophageal corpus 216 µm and isthmus 51 µm long. Œsophageal bulb 70 µm long and 75 µm wide. Nerve ring 137 µm and excretory pore 171 µm from anterior extremity. Vulva 91 µm anterior to anus. Tail 314 µm long.

Paratype males (three specimens) : Length 1.35-1.42 mm. Maximum width 87-99 µm. Buccal cavity 26-29 µm, œsophageal corpus 313-401 µm and isthmus 51-56 µm long. Œsophageal bulb 62-72 µm long and 66-70 wide. Nerve ring 98-152 µm and excretory pore 173-222 µm from anterior extremity. Ventral sucker 27-30 in diameter, 173-216 µm from anus. Spicule 100-115 µm gubernaculum 55-65 µm and tail 162-196 µm long.

Paratype females (three specimens) : Length 1.75-1.83 mm. Maximum width 105-111 µm. First part buccal cavity 15-16 µm, second and third part buccal cavity 50-54 µm, œsophageal corpus 208-233 µm and isthmus 46-55 µm long. Œsophageal bulb 71-74 µm long and 72-74 µm wide. Nerve ring 113-132 µm and excretory pore 154-177 µm from anterior extremity. Vulva 86-124 µm anterior to anus. Tail 309-383 µm long.

CONCLUSIONS

Both sexes are known in only eleven of the twenty-one nominal species of *Heth*. In general, species have been separated on the basis of the cuticular ornamentation on the anterior end of the female. Care must be taken in using this character since in the present study the small button-like formations posterior to the cervical collar commonly became dislodged during manipulation of the specimen. Fortunately, even when dislodged, their position was indicated by the nerve ending which remained in the cuticle.

Although cuticular ornamentation is useful to delineate groups of related species, it is not always sufficient in itself to distinguish such species. Thus, the two species described herein and *H. duvidosum* and *H. perarmatum* are very close in cuticular ornamentation and other characters (e.g. vulvar structure and number of somatic papillae in the female ; spicular structure and disposition of genital papillae in the male) are more useful in distinguishing the species.

As is true in many nematodes the cephalic extremity of the male of *Heth* is more primitive than that of females. Thus, there are no pseudolabia although tissue surrounding the amphids is slightly raised. Cuticular spines are absent ; the mouth opening is hexagonal and the inner ring of papillae is present. Even the three cuticular projections at the base of the buccal cavity are probably primitive characters in the Ransomnematinae (the group in which THEODORIDES (1965) placed *Heth*) since similar structures have been described in males of *H. dimorphum* Chitwood, 1935, and *Brumptaemilius oschei* Dollfus, 1964, and in both sexes of *Ransomnema longispiculum* Artigas, 1926 (see CHITWOOD, 1935 ; DOLLFUS, 1952 ; OSCHE, 1960).

In females, the head is modified by the development of two prominent pseudolabia. These result from hypertrophy of tissue lateral to the mouth but apparently not that surrounding the outer cephalic papillae since these lie at the base of the pseudolabia. The inner papillae have disappeared and the pseudolabia are transformed apically into two large plates which completely cover the cephalic surface. CHABAUD (1958) described similar development of pseudolabia in the Habronematinae (order Spirurida). In this group the pseudolabia " ... se dilatent à l'apex en deux grandes lames qui recouvrent les lèvres primitives ". In the Habronematinae, the outer papillae are on dorsal and ventral lips whereas in *Heth* the primitive lips have completely disappeared.

Associated with the development of the pseudolabia, the buccal cavity of the female becomes highly modified. A prominent anterior segment develops between the pseudolabia. The second part of the buccal cavity, lined by a thickened cuticular ring with three lappet-like formations is presumably equivalent to the posterior portion of the male buccal cavity with its cuticular projections. The third part of the buccal cavity lined by striated cuticle has no equivalent in the male.

It is likely that cephalic modifications in *Heth* play a role in feeding. *Heth* spp. probably feed on the microbial community in the diplopod intestine. Cuticular projections in the buccal cavity of the male would presumably prevent large particles from entering and obstructing the mouth opening. Similarly, the cuticular comb-like lining to the mouth opening in the female would prevent entrance of large particles. The elaborate pseudolabia increase the surface area of the mouth and therefore the rate at which material can be filtered.

Sexual dimorphism is common in nematodes but is rarely as pronounced as it is in *Heth*. Generally it manifests itself late in ontogeny and dimorphic structures exhibit a more primitive or juvenile (paedomorphic) state in the male. Such paedomorphism may result from progenesis as appears to be true in some oxyurids (ADAMSON, 1981). Thus, males reach sexual maturity rapidly and die soon after copulation while still " somatically immature ", whereas the larger females, long-lived as adults, may undergo considerable morphological development during or after the final moult.

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